Banding Patterns in *Haliotis* - II

Some Behavioral Considerations and the Effect of Diet on Shell Coloration for *Haliotis rufescens*, *Haliotis corrugata*, *Haliotis sorenseni*, and *Haliotis assimilis*

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(Plate 17; 1 Table)

INTRODUCTION

In a previous paper (Olsen, 1968) I attempted to develop a technique for using the sequence of colored bands in the shells of *Haliotis rufescens* Swainson, 1822 to trace the seasonal variation in the abundance of *Nereocystis luetkeana* (Mertens) Postels & Ruprecht, 1840, the primary component in the diet of the abalones in Morro Bay (Cox, 1962). *Nereocystis* is a large brown alga that floats well off the bottom. Commercial fishermen make it available to the abalones by cutting the stipes while diving and with the propellers of their boats. I mentioned that this technique could be used to study algal abundance in the abalone's home area and would also be of use to investigators interested in abalone growth rates. In addition, it would be useful in studying seasonal variations in feeding intensity as reported by Ino (1943) and later tied in to seasonal temperature fluctuations by Sakai (1962 a). Abalone growth rate is economically important since *Haliotis* is a widespread genus with some 50 or more species (Sorensen, 1949) and is important in a number of countries including Japan, Australia, South Africa, Mexico, and the United States of America. Forster (1967) discusses the importance of growth rate data in fisheries investigations.

Before the information contained in the banding patterns can be used by sublittoral ecologists certain behavioral information must be considered. The most important aspect to be considered is whether the animals graze the macroalgae in their immediate vicinity or trap food particles which are carried to them by currents and surge. Any attempt to use the banding patterns to study the algal abundance in the abalone's home area would certainly be unsuccessful if the animals were eating food that was carried to them by the current from a distant point.

Haliotis feeding behavior has been reported for a number of species. Cox (1962) says that the red abalone, *H. rufescens,* feeds by extending its epipodium and capturing pieces of macroalgae that float by in the drift. Sinclair (1963) described the grazing of *H. iris* kept in aquaria. She also described populations of abalones living in the New Zealand tidepools where there were no algae available for grazing. She hypothesized that the abalones left these pools at night in order to feed, but it seems possible that they feed by trapping algal debris washed into these pools.

Stephenson (1924) describes the grazing of captive *Haliotis tuberculata* Linnaeus, 1758 in England, but also mentions inducing animals in nature to feed by holding a piece of *Fucus* near the mouth. From these and other studies it appears that although abalones will graze, the normal method of feeding is by capturing particles of macroalgae in the drift.

Cox (1962) reported annual growth of *Haliotis rufescens* of up to 48 mm but says that it is irregular and varies greatly. Leighton & Boolootian (1963) found the annual growth rate of *H. cracherodii* Leach, 1817 to be 20 mm. In England, Forster (1967) found that *H. tuberculata* grew 15 to 16 mm per year. Sakai (1962 b)

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[1] This work was completed while the author was working on the Master of Arts program in the Department of Biological Sciences at the University of California at Santa Barbara. The computer analysis was supported by University of California Committee on Research grant for computer research no. 5997.

found that *H. discus hannai* Ino, 1953 grew an average of 20 mm per year over a 5-year period. Commercial fishermen report annual growth of up to 2 inches (51 mm) but feel that ½ inch (13 mm) is more likely the average figure.

It is the purpose of this paper to supply the behavioral information that is necessary before this shell banding information can be used for dating purposes. In addition, I have presented the results of a series of feeding experiments which were an extension of the diet and shell color studies of Ino (1952), Sakai (1962 a) and Leighton (1961, 1963). A preliminary attempt at taking the yearly patterns of shell colors and utilizing them to group the sample into age classes is also reported.

MATERIALS AND METHODS

Growth was measured by taking the shell band data described in the previous paper and totalling the distance from one red winter band to (but not including) the next. This was done with a simple program on an IBM 360-50 computer.

To study the effects of changes in diet upon shell color, 5 species of abalones were collected by SCUBA divers, brought into the laboratory, placed in 8-liter plastic pans, and maintained at 14 to 20° C in running sea water. I used small individuals because of space limitations and because earlier workers reported a rapid early growth rate. The number of individuals, species, and the size range were as follows: 8 *Haliotis rufescens* (64 to 153 mm), 10 *H. sorenseni* Bartsch, 1940 (64 to 127 mm), 4 *H. assimilis* Dall, 1878 (51 to 102 mm), 3 *H. corrugata* Gray, 1828 (19 to 140 mm), and 1 *H. cracherodii* (33 mm). The animals were fed by placing a liberal quantity of the algae into the tank and leaving it there until it was eaten or until it began to deteriorate. The tanks were cleaned regularly to prevent growth of other species of algae which would contaminate the experiment. The animals were fed one species of alga until there was an obvious area of new shell growth. At this time they were transferred to another condition. They were fed *Macrocystis* as a brown alga, *Gelidium* for red and *Enteromorpha* for green alga.

Behavioral information came from the abalones used in the shell color studies, from a series of simple conditioning experiments run predominantly on red abalones, and from 2 years spent as a commercial abalone fisherman. The behavioral observations were conducted in the following manner: after collection, the abalones were placed in tanks with running sea water; the tanks were 4 x 4 x 1 foot in dimension. The abalones were left alone for 3 or 4 days to acclimate themselves. The experiment itself consisted of touching the epipodial, cephalic, and respiratory tentacles with *Macrocystis*, probes, and in one series, juice from ground *Macrocystis*. Any change in the behavior of the animal was then recorded. Forty *Haliotis rufescens* were used in these experiments.

RESULTS

Annual Growth: There were 361 annual band series (from one red, or winter band, to but not including the next red band) observed in the 45 shells. This gives an average age of the animals used in this study of 8.02 years. There was too much variation in the width of the year bands to group them into well defined year classes. The width of these bands represents one year's growth and the average was 17.13 mm ($S^2 = 256$). The width of these annual bands ranged from 2 mm to 146 mm.

Shell Color and Diet: The results of the feeding - shell color study are listed below and in Table 1 by species. The colors given are comparable to colors listed in Maerz & Paul (1950); the designations in the atlas are given in parenthesis with each color.

Haliotis sorenseni: Red algae in the diet in every case resulted in a deep red color (L-7, p. 36) while brown algae resulted in green-white (G-9, p. 77) or brown-white (I-3, p. 47). The shell color of the Sorensen abalones that were fed green algae was the same green-white as when the animals were fed brown algae. None of the abalones formed blue-grey shell, a color frequently encountered in specimens collected from waters deeper than 15 m.

Haliotis rufescens: New shell growth was red (L-7, p. 36) on a red algal diet. When fed brown algae, animals with shells under 85 mm formed new shell of a pale blue-green color (E-4, p. 77), while the larger animals had shells of brown-white (A-1, p. 47).

Haliotis corrugata: New shell growth of *Haliotis corrugata* was a brown-red (J-12, p. 36) in every case when

Explanation of Plate 17

Figures a to c: Feeding behavior of *Haliotis cracherodii.*
a: Epipodial tentacles are extended into the water in search of food.
b: Contact is made with a piece of *Macrocystis* and the animal extends the foot to capture it. After the food is captured, it is pulled under the foot (c) before the animal commences eating.

Figure d: Defensive behavior of *Haliotis rufescens.*
The epipodial tentacles are extended while the shell is clamped down close to the substrate.
e – epipodial tentacle; f – foot; m – piece of *Macrocystis* frond; r – respiratory tentacle

Figure 1 a

Figure 1 b

Figure 1 c

Figure 1 d

Table 1

Haliotis Shell Color Under Various Algal Diets

Species (sample size)	Red algae	Brown Algae	Green Algae	Diatoms
Haliotis assimilis (4)	red, blue, and white mottled	turquoise and white mottled pale brown orange		
Haliotis corrugata (3)	brown-red	turquoise, white		
Haliotis cracherodii (1)	reddish-brown [1]	blue-black blue-green [1]		blue-green [2]
Haliotis rufescens (8)	red	white blue-green [3] pale green [3] olive green [3]	pale green [3]	
Haliotis sorenseni (10)	red purple [2]	pale green pale brown	pale green	
Haliotis discus hannai	brown [4, 5] yellowish brown [5]	bluish green [4] green [5]	bluish green [4]	bluish green [4]
Haliotis gigantea [5]	brown or yellowish-brown	green		
Haliotis sieboldii [5]	brown or yellowish-brown	brown or yellowish-brown		

[1] Leighton, 1963
[2] Leighton, personal communication
[3] Leighton, 1961
[4] Sakai, 1962a
[5] Ino, 1952

fed red algae. When they were fed brown algae 2 of them (one 19 mm and the other 140 mm) laid down a vivid turquoise shell (I-3, p. 83) and the other (85 mm) laid down a pure white shell.

Haliotis cracherodii: When fed brown algae this abalone laid down the deep blue-black shell described by Leighton, 1963.

Haliotis assimilis: *Haliotis assimilis* was the most variable of the species studied. When fed brown algae individuals with a predominantly blue shell laid down a turquoise and white mottled shell; one individual with a large proportion of red mixed with the blue background laid down a brown and white mottled shell, and one small individual (51 mm) with an orange shell continued to lay down the same color when put on a brown algal diet. When fed red algae the 2 animals with blue and white mottled shells laid down shells which were red and white and blue mottled. No results were obtained for red algae from the other *H. assimilis*.

Behavior: The first behavioral action was noticed when the abalones were brought in from the field. At this time they would draw the shell down as close as they could to the substrate and extend their epipodial tentacles as is shown in Plate 17, Figure 1 d. They would wave these tentacles rapidly through the water. If the animal was disturbed further, it would retract the tentacles and clamp the shell down to the substrate.

Feeding behavior was similar to that described by Cox, 1962. The animal would raise its shell and extend the cephalic and epipodial tentacles into the water (Plate 17, Figure 1 a). When a piece of alga touched one of these tentacles (Plate 17, Figure 1 b), the abalone turned and extended the foot in the direction of the contact. At the same time tentacular waving would increase and consequently there was an increased number of contacts between the tentacles and the food. Once the foot made contact with the alga, it pulled the piece under the shell and the animal began eating (Plate 17, Figure 1 c). Some abalones held food in this position for 12 hours without eating it. This feeding behavior occurred in all of the species used in the diet - shell color experiments and invariably in the 40 *Haliotis rufescens* studied. Feeding could be stimulated by a variety of stimuli, among them water current and light. A successful attempt at conditioning red abalones was made using light as the stimulus and will be reported in a later paper.

Small abalones (40 mm and under) probably do feed primarily by grazing since they are found under rocks and in cracks where drift algae are seldom available. In abalone cultivation efforts they are frequently fed crustose calcareous algae which are found on rocks. Abalones can distinguish the difference between food particles and nonfood particles with their tentacles but not with their foot. If a glass probe, a finger or any other non-food substance